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International Journal for Parasitology 32 (2002) 245–254

INTERNATIONAL Journal for PARASITOLOGY

www.parasitology-online.com

Invited review

The evolution of monogenean diversity

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Received 10 April 2001; received in revised form 10 September 2001; accepted 28 September 2001

Abstract

The Monogenea are an ideal group for investigations of the processes behind their past diversification and their present diversity for at least three reasons: they are diverse both in terms of morphology and numbers, they are generally host specific, and their phylogeny is well resolved, at least to the family level. The present investigation takes a broad look at monogenean diversity in order to try to determine whether the diversification of monogeneans is driven by some ecological features of the parasites themselves, or by extrinsic factors associated with their hosts. First, our current knowledge of monogenean diversity appears good enough to warrant investigation into its evolution. The body size of new species correlates negatively with their year of description both generally and within given families, i.e. it decreases over time in a way that suggests that only some of the smallest species are left to be discovered. Second, the occurrence of congeneric monogenean species on the same host species is not associated with host body size, once phylogenetic influences are controlled. This analysis suggests that host size is not one of the factors promoting local diversification of monogenean taxa. Third, the species richness of the different monogenean families does not correlate with the average body size of their members. Thus, this basic parasite life-history trait is not a determinant of diversification rates. Combined, the results of these separate analyses provide preliminary answers to some of the big questions concerning the diversification of monogeneans, but leave many other questions unanswered. The phylogenetic analytical framework adopted here should allow these questions to be tackled once the necessary data become available. © 2002 Australian Society for Parasitology Inc. Published by Elsevier Science Ltd. All rights reserved.

Keywords: Body size; Congeneric species; Phylogenetic effects; Speciation; Sympatry

1. Introduction

Estimating the present diversity of organisms and how it is maintained, and understanding how they diversified in the past, are the new cornerstones of conservation biology, ecology and evolutionary biology. Given that parasites account for a considerable proportion of existing biodiversity, these questions are increasingly being asked in relation to parasitic organisms (Brooks and Hoberg, 2000; Poulin and Morand, 2000). The study of past parasite diversification and present parasite biodiversity is still in its infancy, however.

The Monogenea are an ideal parasite taxon for investigations of past diversification and present diversity for at least three reasons. First, monogeneans are a diverse group, with several thousand species currently described. Brooks and McLennan (1993a) suggested that the Monogenea are the only clade among the parasitic flatworms to have undergone an adaptive radiation (but see Rohde, 1996). Monogeneans are diverse not only in terms of numbers but also with respect to their morphology and ecology: from an ancestor parasitic on the skin of early vertebrates, monogeneans have expanded to colonize internal as well as external organs of a range of living aquatic vertebrates, and now display a variety of designs (Kearn, 1994; Whittington et al., 2000). Second, the phylogeny of monogenean families is well resolved (Boeger and Kritsky, 1993, 1997; Mollaret et al., 2000), and the elucidation of within-family relationships is well under way (e.g. Sinnappah et al., 2001). A good knowledge of the relationships among members of a clade, especially among higher taxa such as families, is essential for the study of diversity using modern comparative methods (Poulin, 1995; Sasal and Morand, 1998). Third, monogeneans tend to be host specific, i.e. each monogenean species infects only one or very few host species (Poulin, 1992; Sasal et al., 1999). This is not necessarily the outcome of strict cospeciation between the parasites and their hosts, although this has been documented in monogeneans (Desdevises et al., 2000). There is also evidence of host switching during the coevolutionary history of monogeneans and their hosts, from studies both at the level of sister species (e.g. Guégan and Agnèse, 1991) and among more basal branches in the monogenean phylogeny (Boeger and Kritsky, 1997).

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PII: S0020-7519(01)00329-0

The high host specificity shown by most monogeneans, however, makes it easier to search for a link between the ecological characteristics of the hosts and the diversity of their monogenean parasites, and to control for the phylogenetic history of their associations.

In this paper, I will take a broad look at monogenean diversity in order to try to determine whether the diversification of monogeneans is driven by some ecological features of the parasites themselves, or by extrinsic factors associated with their hosts or their external environment. I will use various databases and apply modern comparative methods as much as possible (Sasal and Morand, 1998). Any such attempt at general answers is bound to be met with criticism: exceptions can always be found to the general trends that emerge from comparative analyses. In a sense, the analyses presented here can be viewed as preliminary. My aim, though, is to provide tentative answers to some big general questions, and not to find definitive answers to specific questions. The broad patterns, if any, that emerge from the comparative analyses can be used to generate hypotheses about the evolutionary processes that promote monogenean diversification, hypotheses that can then be tested in specific systems.

Three separate investigations are combined here to tackle the issue of monogenean diversity. First, it is important to assess how good our estimates of monogenean diversity really are, and I will try to evaluate how far we are from a complete inventory of living monogenean species. Any attempt to understand the diversification of a group must be based on reasonably comprehensive estimates of the group's diversity, and I will thus, as a first step, make sure we know enough about monogenean diversity to study its determinants. Second, I will focus on congeneric monogenean species that exploit the same host species, and attempt to determine whether one external factor, namely the size of the host, can promote the coexistence of closely related species. The assumption here is that congeneric species on the same host are sister species, and that their occurrence is the result of an intrahost speciation event. Third, I will verify whether the species richness of the different monogenean families correlates with the average body size of their members, to see whether this basic parasite life-history trait is a determinant of diversification rates.

2. How well do we know monogenean diversity?

We do not have a complete inventory of existing monogenean species, and we will not have one for many years, if ever. Is it therefore valid to investigate patterns of diversity in monogeneans if we do not yet have a complete list of living species? The answer depends on how close we are to completing the list. There are some indirect ways of assessing our knowledge of existing species in a particular group. One method is to examine the relationship between the body size of known species and the year in which they were first described. In many taxa, recently described species tend to be of smaller size than previously recognised species, simply because the probability of detection increases with body size (Gaston, 1991; Gaston and Blackburn, 1994). In the early years of scientific investigation, both small and large species are found and described formally; as time goes by, all the large species are known and the only ones left to be documented are the small ones. The efficiency of the numerous methods used to collect ectoparasites on fish varies greatly (see Grutter, 1995), and it is likely that earlier surveys based on visual inspection of the host missed many of the smaller parasites. Using this approach with parasitic copepods, Poulin (1996a) found a negative correlation between parasite body size and year of description among copepod species parasitic on fish hosts, but there was no relationship between these variables among copepod species parasitic on invertebrate hosts. These results mean that we have achieved a good inventory of copepods parasitic on fish, since only the small species are left undiscovered, whereas our knowledge of copepods parasitic on invertebrates is much more patchy and many large-bodied species are yet to be recorded even today.

Here, I will proceed with a similar analysis on monogenean species. If no relationship is observed between the body size of monogenean species and their year of description, it will mean that we are a long way from a complete inventory, even of the relatively large-bodied species. If, on the other hand, a negative correlation is observed between body size and year of description, it will indicate that we have reached a point where only some very small species are left undiscovered. Any conclusion will only be based on existing data, of course, but I assume that its implications would extend to the yet-to-be-discovered monogenean fauna.

2.1. Methods

Data on body sizes of monogenean species described before 1963 were obtained from Yamaguti (1963), and those from monogenean species described since then were obtained from original species descriptions published in four selected journals: *Journal of Parasitology*, *Journal of Helminthology*, *Proceedings of the Helminthological Society of Washington*, and *Folia Parasitologica*. Yamaguti (1963) did not present body size data for all the species he compiled, and the four above journals do not account for all species described since the 1960s, but together these sources provide a representative sample. Monogenean body size was taken as total body length; when a range was provided instead of a mean or a single measurement, the midpoint was used. In some monogenean taxa (e.g. Capsalidae), the body of the worm is almost as wide as it is long, and body length is a poor surrogate for actual body size; however, it is useful in the present analysis since the probability of detection is probably proportional to the largest linear dimension of a worm.

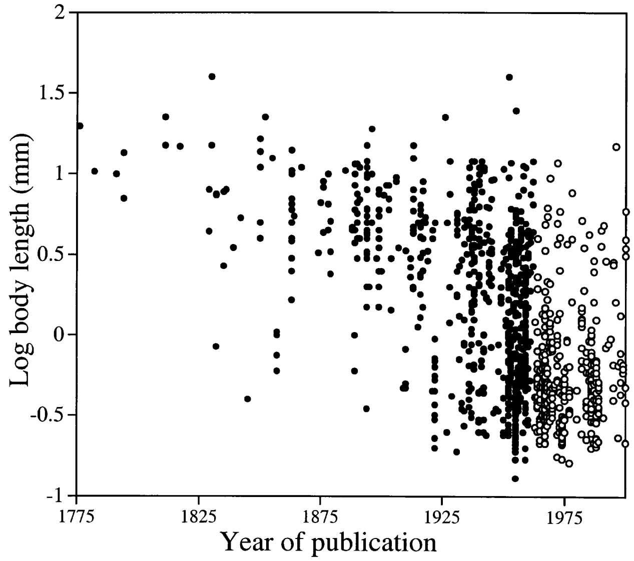

Fig. 1. Body length of 1131 monogenean species as a function of the year in which they were described. Different symbols are used to indicate species listed in Yamaguti's monograph (Yamaguti, 1963) (●) and those described after 1963 (○).

The data on body sizes were log-transformed and analysed in two ways. First, a correlation coefficient was computed between monogenean body size and year of description; this was done for the entire data set and for relevant subsets of the data. Second, to account for potential phylogenetic effects, comparisons were performed within families. More specifically, body sizes of all species in a family described before 1962 were compared to those of species in the same family described after 1963, using two-tailed *t*-tests. This was done for the few monogenean families for which sufficient data were available, i.e. at least five species described in each of the two periods.

2.2. Results and discussion

Overall, data on body size were obtained for 1131 monogenean species. Across all these species, there was a strong negative correlation between body size and year of description ($r = -0.558$, $P = 0.0001$). The year in which species are described explains a little over 30% of the variance in their body size. In fact, the scatter of points has a roughly triangular shape (Fig. 1), which suggests that the correlation is mainly due to the sudden inclusion, beginning in the 1950s, of the small-bodied monogeneans (<1 mm in body length, mainly dactylogyrids and gyrodactylids) in the published record. This means that by the time of Yamaguti's monograph (Yamaguti, 1963), the smallest monogenean taxa were already known to a certain extent. Indeed, the negative correlation between body size and year of description found across all species remains when only the pre-Yamaguti species are included ($n = 735$, $r = -0.486$, $P = 0.0001$) but is replaced by a positive, though weaker, relationship among the post-Yamaguti species ($n = 396$, $r = 0.134$, $P = 0.0074$).

Clearly, if the inclusion of small-bodied monogenean taxa can change the nature of the relationship between body size and year of description, an analysis across species from different families may suffer from phylogenetic influences. To eliminate these potential effects, the correlation analysis was repeated within all monogenean families for which more than 15 species were available in the data set. In all 13 families for which this was possible, negative correlations were found between body size and year of description, though the correlations were only statistically significant in seven of the 13 families (Table 1). Therefore, the negative relationship exists to some extent within monogenean families as well as across all species. Another way to test this is to compare the body size of pre- and post-Yamaguti species. In the six families for which this was possible (because they included at least five species described in each of the two periods), species described pre-Yamaguti were larger than those described post-Yamaguti in five families, and significantly so in three families (Fig. 2).

The general pattern is thus one where the species currently being described are smaller than those previously known. Of course, there is a minimum viable body size for monogeneans, which, based on present evidence, is somewhere around 0.15 mm in length. We should not expect to find species smaller than this size, but we should expect to find many more species of this or a slightly larger size. In addition to our general lack of information on small-bodied monogenean species, there may also be a geographical component to our incomplete knowledge of monogenean diversity. For instance, monogeneans infecting tropical fish (or deep-water fish) are most likely not as well surveyed as those of temperate fish or commercially important fish species. What we know of tropical monogeneans may be biased, too: because of the efforts of a small group of dedicated systematists, we know many species from relatively small geographical areas, but very little from most other areas. Still, it appears that we have achieved a reasonably good knowledge of monogenean diversity, and although many species are yet to be discovered and described, we

Table 1
Relationships between body size and year of description for various monogenean families

Family	No. of species	Size range (mm)	*r*	*P* value
Axinidae	29	1.60–8.10	−0.337	0.0735
Capsalidae	51	0.90–22.5	−0.736	0.0001
Dactylogyridae	462	0.13–4.97	−0.195	0.0001
Diclidophoridae	20	0.99–10.0	−0.367	0.1113
Diplectanidae	51	0.32–1.66	−0.215	0.1291
Discocotylidae	19	1.36–19.0	−0.537	0.0177
Gastrocotylidae	25	1.40–12.0	−0.055	0.7930
Gyrodactylidae	132	0.20–3.30	−0.022	0.8064
Hexabothriidae	27	1.62–22.5	−0.513	0.0062
Mazocraeidae	31	0.51–12.5	−0.561	0.0010
Microcotylidae	75	1.15–15.0	−0.446	0.0001
Monocotylidae	34	0.48–12.0	−0.555	0.0007
Polystomatidae	31	1.50–10.0	−0.222	0.2290

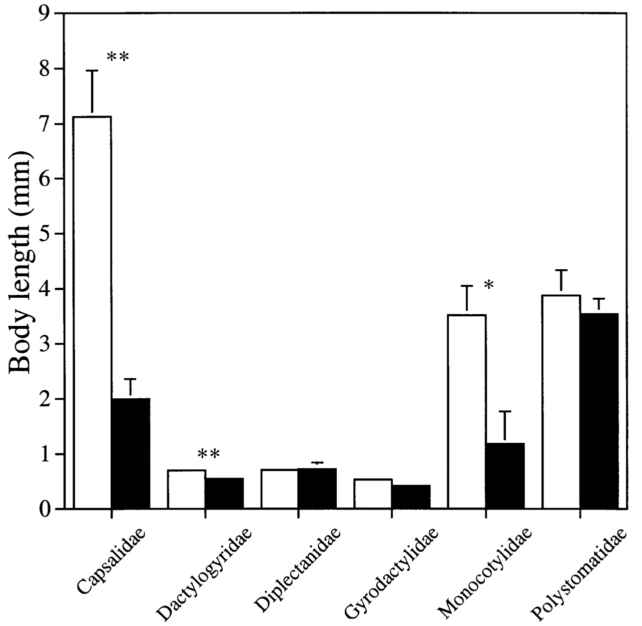

Fig. 2. Mean (±SE) body length of monogenean species described pre-1963 (white bars) and post-1963 (black bars) for the six families for which there were sufficient data. Numbers of species included per family are given in Table 1. Asterisks indicate significant differences between means (*t*-tests on log-transformed data: *$P < 0.01$; **$P < 0.005$).

currently have enough information to start asking questions about monogenean diversification.

3. Coexistence of congeneric monogeneans

The number of free-living species coexisting in a given area is the product of two sets of processes (Rosenzweig, 1995). On an ecological time scale, the number of species in an area reflects an equilibrium between the rates of colonisation from outside areas and the rates of extinction. On an evolutionary time scale, new species can also be generated internally by speciation. Similar processes also act to determine the richness of parasite species exploiting a host population. In the context of the diversification of a parasite lineage, it is intrahost speciation that is of interest. Allopatric speciation, in all its forms, is likely to be the main mode of speciation in parasites in general. It has been suggested, however, that sympatric speciation is more likely in monogeneans than in other parasite groups, because of some of their biological features such as a direct life cycle and the relatively long life span of their hosts (Brooks and McLennan, 1993b). Congeneric monogenean species exploiting the same host may represent cases of sympatric (or intrahost) speciation. Kennedy and Bush (1992) suggested that the presence of multiple congeneric parasite species in a host population may represent cases of species flocks, resulting from a small-scale radiation event. They included dactylogyrid monogeneans among the few parasite taxa in which these species flocks are common. For many other groups of monogeneans parasitic on fish, opportunities for sympatric speciation should also be numerous, with many potential niches (i.e. infection sites) left completely vacant (Rohde, 1979, 1994). The key assumption here is that congeneric species on the same host are sister species, and that their occurrence is the result of one or more intrahost speciation events. This may not always be the case. For instance, among polystomatid monogeneans, congeneric species infecting the same site, even in phylogenetically and geographically distant host species, are more closely related than congeneric species infecting different sites on the same host species (Littlewood et al., 1997). Thus, all instances of congeneric monogeneans on the same host cannot naively be interpreted as examples of intrahost or sympatric speciation.

If congeneric monogeneans are the product of sympatric speciation, however, what factors may promote this type of speciation? One factor may be host body size, which is often a good predictor of species richness in parasite communities in general (Poulin, 1997; Morand, 2000) and monogenean communities in particular (Guégan et al., 1992; Sasal et al., 1997). Many arguments derived from island biogeography theory or epidemiological models can be used to explain this pattern. Simply put, larger-bodied host species offer a greater surface area for parasite attachment, possibly a greater variety of niches, and less ephemeral habitats since they live longer than small-bodied hosts. These features should favour sympatric speciation, decrease the risk of extinction, and facilitate the coexistence of related species.

Here, I investigate the patterns in the occurrence of congeneric monogeneans in ectoparasite communities of fish. Initially, I examine whether the occurrence of congeneric monogeneans is associated with host body size, regardless of host phylogeny; this allows a quantitative description of the present-day distribution of congeners in relation to host size. Then, in a comparative analysis which controls for host phylogeny, I re-examine this relationship in a way that allows a better assessment of the potential *causal* influence of host body size on the diversification of monogeneans over evolutionary time.

3.1. Methods

The analysis focused on the monogenean parasites of Canadian freshwater fish, for which there exists substantial information. From the survey by Beverley-Burton (1984), I recorded the number of monogenean species, the number of monogenean genera, and the number of genera represented by more than one species, for each fish species from which at least two monogenean species have been recorded. Mentions of monogeneans not identified to the species level were excluded. The great majority of monogenean species parasitic on Canadian freshwater fish are specific to a single host species or to two closely related species (Poulin, 1992), thus I did not include host specificity as a potentially confounding variable.

For each fish species, total body length (obtained from

Scott and Crossman, 1973) was also recorded. Finally, an estimate of study effort was also obtained for each fish species. In most studies of parasite species richness, host-sample size or other measures of host-study effort often have a strong influence on the number of known parasite species per host species (Walther et al., 1995), and must be considered as a confounding variable. Thus, I used the average number of articles published per year on each fish species over a 10-year period, obtained from Cvancara's compilations (Cvancara, 1984–1993), as an independent index of our knowledge of each fish species.

All data were log-transformed. The first analysis simply determined whether fish body size is correlated with within-genus monogenean diversification. Treating host species as independent observations ignores the potentially strong influence of phylogeny, but allows one to find out whether host size is associated with higher rates of monogenean diversification. The number of monogenean species per fish species was regressed against the number of monogenean genera per host species, and residuals of this regression were used as measures of the *relative* number of monogenean species per monogenean genus. Positive residuals indicate that there are more congeneric monogeneans on a fish species than expected on average, whereas negative residual values indicate that there are fewer than expected. Similarly, the number of monogenean genera represented by more than one species was regressed against the number of monogenean genera per host species, with the residuals used as measures of the *relative* number of multi-species genera per host species. These relative values were then used as dependent variables in multiple regressions, with host body length and host study effort as predictor variables.

The subsequent analysis controlled for phylogenetic influences. This approach is more robust when determining whether host-body size has been a *causal* factor in the diversification of monogeneans, because it eliminates relatedness among hosts as a source of pseudo-replication and focuses only on evolutionary instances of divergence (Harvey and Pagel, 1991). I used the phylogenetically independent contrasts method (Felsenstein, 1985) on log-transformed data, implemented using the software package CAIC v.2.0 (Purvis and Rambaut, 1994). The phylogeny of fish species used here is based on several recent references (see Poulin et al., 2000, for further details). Contrasts in relative number of monogenean species per genus, and in relative number of multi-species genera per host species, were first corrected for contrasts in host-study effort, again using residuals from a regression (through the origin; see Garland et al., 1992), and then separately correlated with contrasts in host-body size.

3.2. Results and discussion

Data were obtained for a total of 68 fish species. The number of monogenean species per host species ranged from two to 13, and the number of multi-species genera ranged from zero to three per host species. The number of monogenean genera per host species correlated strongly with both the number of species per host ($r = 0.743$, $P = 0.0001$) and the number of multi-species genera per host ($r = 0.312$, $P = 0.0096$), which justified the use of relative values for these two parameters.

In the multiple regressions across host-species values, the relative number of monogenean species per genus covaried negatively with host size ($r = -0.277$, $P = 0.0405$) and positively, though not significantly, with study effort ($r = 0.233$, $P = 0.0827$). The same patterns were found in the multiple regression using the relative number of multi-species genera per fish species as a dependent variable (host size: $r = -0.269$, $P = 0.0423$; study effort: $r = 0.336$, $P = 0.0120$). Thus, contrary to the initial prediction, multiple congeners appear more common on smaller hosts than on larger hosts. How could small host body size promote monogenean diversification?

Before attempting to explain this pattern, one must first rule out the possibility that it is a phylogenetic artefact resulting from the over-representation of certain host taxa. In the analysis based on phylogenetically independent contrasts, once the effect of host-study effort has been removed, there remains no relationship between host-body size and either the relative number of monogenean species per genus ($n = 64$ sets of contrasts, $r = -0.060$, $P = 0.6373$) or the relative number of multi-species genera per fish species ($r = -0.159$, $P = 0.2093$). In other words, large-bodied host species are not more or less likely to harbour multiple congeners than their small-bodied sister species (Fig. 3), and the patterns found in the cross-species analyses were not a reflection of processes acting over the evolutionary history of host lineages.

It is often difficult to distinguish between factors *associated* with high rates of diversification, and factors *causing* this diversification. In this case, as in an earlier study of the occurrence of congeners among intestinal helminths (Poulin, 1999), a pattern found in a simple analysis across host species disappeared after controlling for host phylogeny. In my view, this rules out host-body size as an important factor determining the rate of intrahost (or sympatric) speciation in monogeneans. The influence of host-body size on species richness in monogenean communities (Guégan et al., 1992; Sasal et al., 1997) may thus be mainly the product of higher colonisation rates on larger hosts. Rates of monogenean diversification per se remain unexplained.

An important factor may be latitude and its relationship to water temperature. Latitudinal gradients in species richness are well documented for a wide range of taxa (Rosenzweig, 1995), but their causes remain unclear. Rohde (1992, 1999) suggested that higher species richness at low latitudes is mainly due to a temperature-mediated gradient in effective evolutionary time, with evolution and speciation proceeding at higher rates in warm areas. Whatever the primary cause for latitudinal trends in species richness, they apply to monogeneans as well, with the species richness of mono-

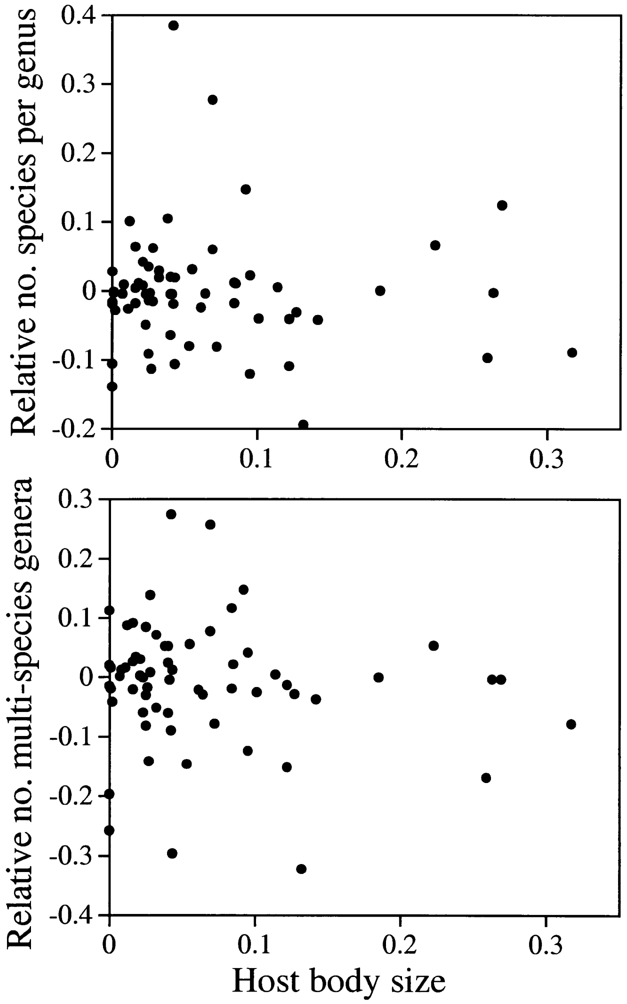

Fig. 3. Number of monogenean species per genus, and number of multi-species genera per host-fish species, as a function of host-body size. Each of the 64 points represents the value derived from a phylogenetically independent contrast between sister fish taxa; values on the *y*-axes have been corrected for study effort.

genean communities of marine fish peaking in the tropics (Rohde, 1993; Poulin and Rohde, 1997). Unfortunately, I could not find a data set large enough to test the idea that congeneric monogeneans are more frequent in tropical habitats.

This suggestion and other related hypotheses remain untested, but point to the value of monogeneans as model organisms for studies of diversification. Recent theoretical models have revived interest in sympatric speciation among evolutionary biologists by showing that the process is plausible under certain conditions, many of which may apply to monogenean populations (Dieckmann and Doebeli, 1999; Kondrashov and Kondrashov, 1999; Via, 2001). Situations in which congeneric species coexist in the same habitat (or on the same host) may be prime examples of sympatric speciation at work, although other explanations are possible (see Brooks, 1979). Some studies have shown, however, that pairs of coexisting congeneric species are not necessarily sister species issued from sympatric speciation events; this applies to polystomatid monogeneans (Littlewood et al., 1997) as well as other organisms (e.g. Coyne and Price, 2000). It is therefore important to keep in mind that the co-occurrence of congeners may be the outcome of other evolutionary events.

4. Monogenean body size and diversification

The previous section examined the potential influence of an external force (host-body size) on monogenean diversification. There may also be properties of monogeneans themselves that could affect the rates at which they speciate and diversify. In particular, differences among monogenean families could determine which families will proliferate and which will not. In most groups of organisms, species richness is not distributed evenly among related taxa: typically, some families contain much more species than related families (Dial and Marzluff, 1989). It is tempting to ascribe the numerical dominance of a few diverse taxa over the many species-poor ones to some biological features that they possess and which allows them to diversify rapidly. Body size is commonly identified as a correlate of numerical dominance. The body-size distribution of most animal taxa is right-skewed, even on a logarithmic scale, such that the smaller size classes contain more species than the larger ones (Blackburn and Gaston, 1994). This is the case in monogeneans (Poulin, 1996b; Poulin and Morand, 1997), although the skew is not as strong as in other taxa and there is even a hint that the distribution of monogenean body sizes is bimodal (Fig. 4). Still, there are clearly more small-bodied monogenean species than large-bodied ones,

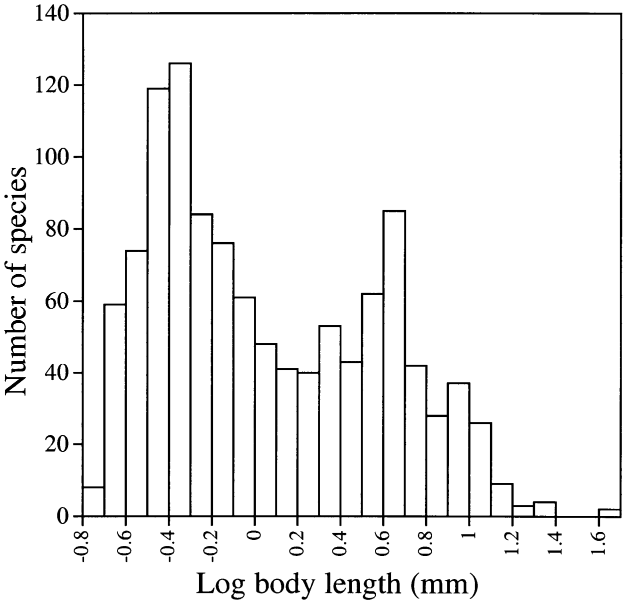

Fig. 4. Frequency distribution of monogenean body sizes among the 1131 species compiled for Fig. 1. Monogenean body-length data are log-transformed, thus a value of 0 indicates a body length of 1 mm.

within the size range shown by these parasites (Poulin, 1996b). What factors could promote the high diversity of small-bodied organisms relative to their larger relatives? The shorter generation times of smaller-bodied organisms can speed up evolution, accelerate speciation and reduce extinction risks (Dial and Marzluff, 1988; Marzluff and Dial, 1991). Habitat heterogeneity, and thus the number of available niches, may also increase with decreasing body size (Fenchel, 1993). These and other processes may facilitate the diversification of smaller organisms relative to that of their larger relatives.

Here, I test for a relationship between the average body size of monogenean families and the number of genera and species they include. A negative relationship would provide support for the role of monogenean body size as a driving force behind monogenean diversification.

4.1. Methods

Data on body sizes of monogenean species were obtained from Yamaguti (1963). Monogenean body size was taken as total-body length; when a range was provided instead of a mean or a single measurement, the midpoint was used. Average body sizes were first obtained for each genus by averaging species values, then family values were obtained by averaging generic values. Data on number of species and genera for each family were also obtained from Yamaguti (1963); although this compilation is not up-to-date, it still provides relative estimates of within-family diversity that are useful for comparative purposes (I could not find a more recent and similarly comprehensive survey of monogenean diversity). In addition to actual numbers of species and genera per monogenean family, the ratio of species number to genera number within each family was also used as a measure of diversification.

All data were log-transformed prior to analysis. First, simple correlations were computed between family body size and either number of species, number of genera, or species-to-genera ratio. This was done across monogenean families without correction for phylogenetic influences. Second, the analyses were repeated using phylogenetically independent contrasts (Felsenstein, 1985), to control for possible phylogenetic effects on diversification. Contrasts were derived from the phylogeny of monogenean families proposed by Boeger and Kritsky (1997). Relationships between family body size and the species-to-genera ratio were performed using the software package CAIC v.2.0 (Purvis and Rambaut, 1994). Relationships between family body size and either the number of species or genera per family (the latter two variables being untransformed), however, were computed using the software MacroCAIC v.1.0.1 (written by Agapow et al., available at http://www.bio.ic.ac.uk/evolve/software/macrocaic). MacroCAIC allows one to test whether species richness is associated with traits such as body size; it does not treat the species richness of a clade as other continuous variables, computing the value for species richness at a node in the phylogeny as the sum, and not the average, of lower branches (Desdevises et al., 2001). All correlations among phylogenetic contrasts were forced through the origin (see Garland et al., 1992).

4.2. Results and discussion

Data were obtained for 39 monogenean families (the same families used for different purposes in Poulin, 1996b). Across these families, there were negative but non-significant correlations between family body size and the number of species per family ($r = -0.125$, $P = 0.449$), the number of genera per family ($r = -0.053$, $P = 0.747$), and the species-to-genera ratio ($r = -0.205$, $P = 0.211$). In plots of these relationships (Fig. 5), points for the Dactylogyridae and Gyrodactylidae are located in the upper left-hand corner, as expected given the typical size and diversity of these taxa. From the phylogeny of these families, 36 sets

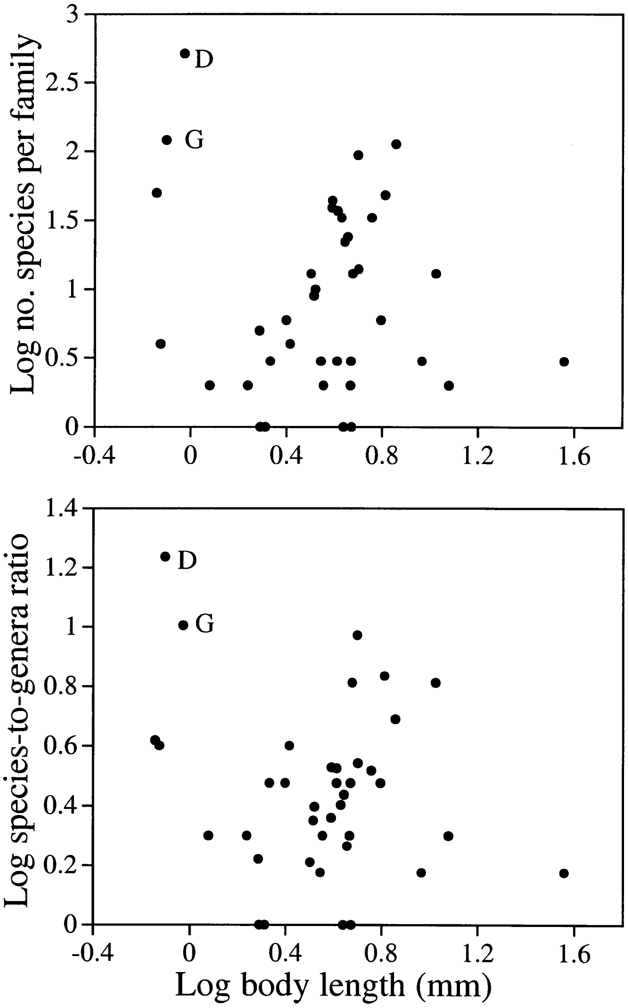

Fig. 5. Number of species per monogenean family, and number of species to number of genera ratio, as a function of mean family body length, for 39 monogenean families. The point (D) in the upper left-hand corner of both graphs represents the Dactylogyridae, and the one (G) below it the Gyrodactylidae.

of independent contrasts could be derived, and the relationships between body size and the three measures of diversification were again non-significant (all $P > 0.25$). The results of the analyses across family values are therefore not phylogenetic artefacts.

Thus there is no solid evidence that the typical body size in a monogenean family is a determinant of the diversification rate within this family. What could explain this? Given the evidence from other groups of organisms and the frequency distribution of body sizes within the Monogenea (Fig. 4), one would expect body size to be linked with rates of speciation and diversification. Not counting the possibility that the data were too imprecise, there are at least three, non-mutually exclusive, explanations for the present results. First, body size per se may be unimportant, but indirectly related to other important characteristics of the family. For instance, dactylogyrids typically live between the secondary gill lamellae of their fish hosts; it may be the use of this microhabitat that has allowed them to diversify, and not their body size itself. This would still generate skewed body-size distributions with a peak among small-bodied size classes (Fig. 4) without body size being the direct, causal factor. Similarly, the other peak in the size distribution of monogeneans (Fig. 4) could represent another minor radiation among taxa exploiting different, larger-grained microhabitats, such as external surfaces and body orifices. Selection may thus favour very small as well as mid-sized monogeneans not because of an advantage of their size per se, but because there happens to be more empty niches for these size ranges to exploit. In fact, however, the two peaks in the body-size distribution of Fig. 4 correspond roughly to the two major branches of the Monogenea, the Monopisthocotylea and the Polyopisthocotylea, and thus provide some evidence that they are distinct, at least from an ecological perspective.

Second, families are to some extent arbitrary taxonomic units. Many currently recognised families were in the past considered as subfamilies or superfamilies. Similarly, the number of genera in a family may be artificially inflated when a genus is split into two genera merely because it contains too many species. There is a hint that this may be happening in monogenean systematics, with a clear correlation among the 39 families included here between the mean number of species per genus and the number of genera per family ($r = 0.474$, $P = 0.0023$). In an analysis of the determinants of species diversification, proper clades are necessary as independent observations, but these do not all have to be presently recognised as separate genera or families. It is possible to define actual clades in the phylogeny of monogenean families of Boeger and Kritsky (1997) that will generate significant negative correlations between clade body size and diversity. These would be just as arbitrary as presently-accepted families, and without objective taxonomic units for this analysis, the role of body size in monogenean diversification will be difficult to evaluate.

Third, monogenean body size is expected to have a role in monogenean diversification if all else is equal. However, the species richness of the different monogenean families may also correlate with the species richness of the host taxa they exploit, which could constrain the number of opportunities for diversification. Without controlling for this other variable, it is impossible to rule out an effect of monogenean body size. Thus the preliminary analysis presented here provides a framework for the analysis of monogenean diversification, but would require more complete data to provide an answer to the question regarding the role of monogenean body size.

5. Conclusions

The Monogenea comprise a diverse, monophyletic group of species that may be the product of an adaptive radiation (Brooks and McLennan, 1993a; but see Rohde, 1996). Here, I have shown that we have achieved a reasonably good knowledge of the diversity of this group, based on the fact that we are mainly left with the very small species to find and describe. It is therefore not premature to attempt to elucidate which ecological and evolutionary forces have driven the diversification of the group. Despite some weak patterns, the analyses presented here provided no strong support for either a role of host size in facilitating sympatric (or intrahost) monogenean speciation, or for a role of monogenean body size in promoting within-family diversification. There is thus much left to investigate about monogenean diversity.

One general weakness of the analyses presented here is the data on which they are based. The data sets are patchy and not always up to date. In particular, there must exist huge numbers of unknown monogenean species in the less well-explored tropical regions, and it is possible that including data from these species when they become available will alter the results of the analyses presented here. However, if the patchiness does not affect certain taxa more than others, this criticism is largely irrelevant if significant trends emerge from the analyses. If a signal can be detected through the noise, surely it cannot be dismissed because the coverage of the data set does not extend to all living species. Most of the key results presented here, though, were non-significant patterns, suggesting that data quality may have been a problem. The phylogeny-based framework used in this study, however, provides a model for future investigations of monogenean diversification, applicable now to certain groups for which better data may be available, or later to the whole group when more comprehensive data are compiled.

Acknowledgements

I thank Ian Whittington and Leslie Chisholm for their invitation to participate in the Symposium, and Serge Morand and two anonymous referees for commenting on a first draft of the manuscript.

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